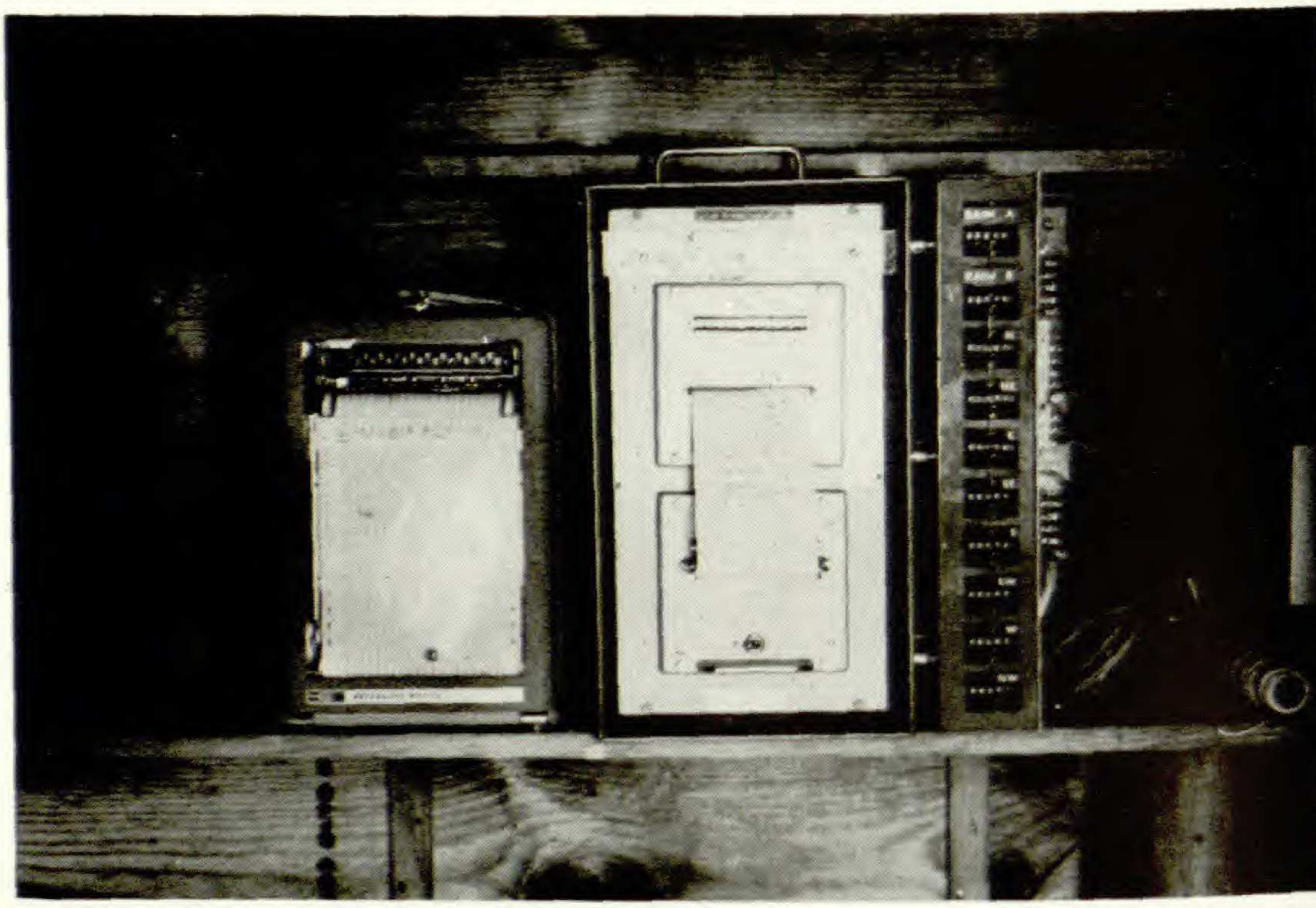

FIG. 2. From left to right the instruments are: event recorder, impulse printer, and accumulating counters. The counters registered total rainfall and wind direction.

whole inch of rain were also recorded by the event recorder to provide for better resolution of the data during heavy rain. As the study progressed and equipment deteriorated, the redundancy of the two records minimized gaps in the records of wind and rain. Each bucket tip in the cloud-water collector, equal to 50 milliliters of cloud water per square meter of collecting surface, caused a switch closure that was recorded by another pen of the 20-pen event recorder.

RESULTS

Rainfall. Various factors may affect the rainfall of Pico del Oeste. It is near enough to the sea to respond to tropical maritime influences. Kraus (1963) found that maritime precipitation is significantly more frequent at night; Alaka (1964) reports the widely held belief that precipitation is suppressed during midday over the tropical oceans. The peak is also far enough inland to be affected by convective showers, high enough to experience orographic rainfall, and of course subject to synoptic scale weather disturbances. These assorted conflicting influences explain why an analysis of the diurnal variation of rainfall showed three maxima and three minima, all of uncertain significance.

However, when the frequency of occurrence of rain and the intensity of the actual rainfall occurrences were analyzed separately a clear picture emerged as shown in FIGURE 3. Rainfall was almost twice as frequent at

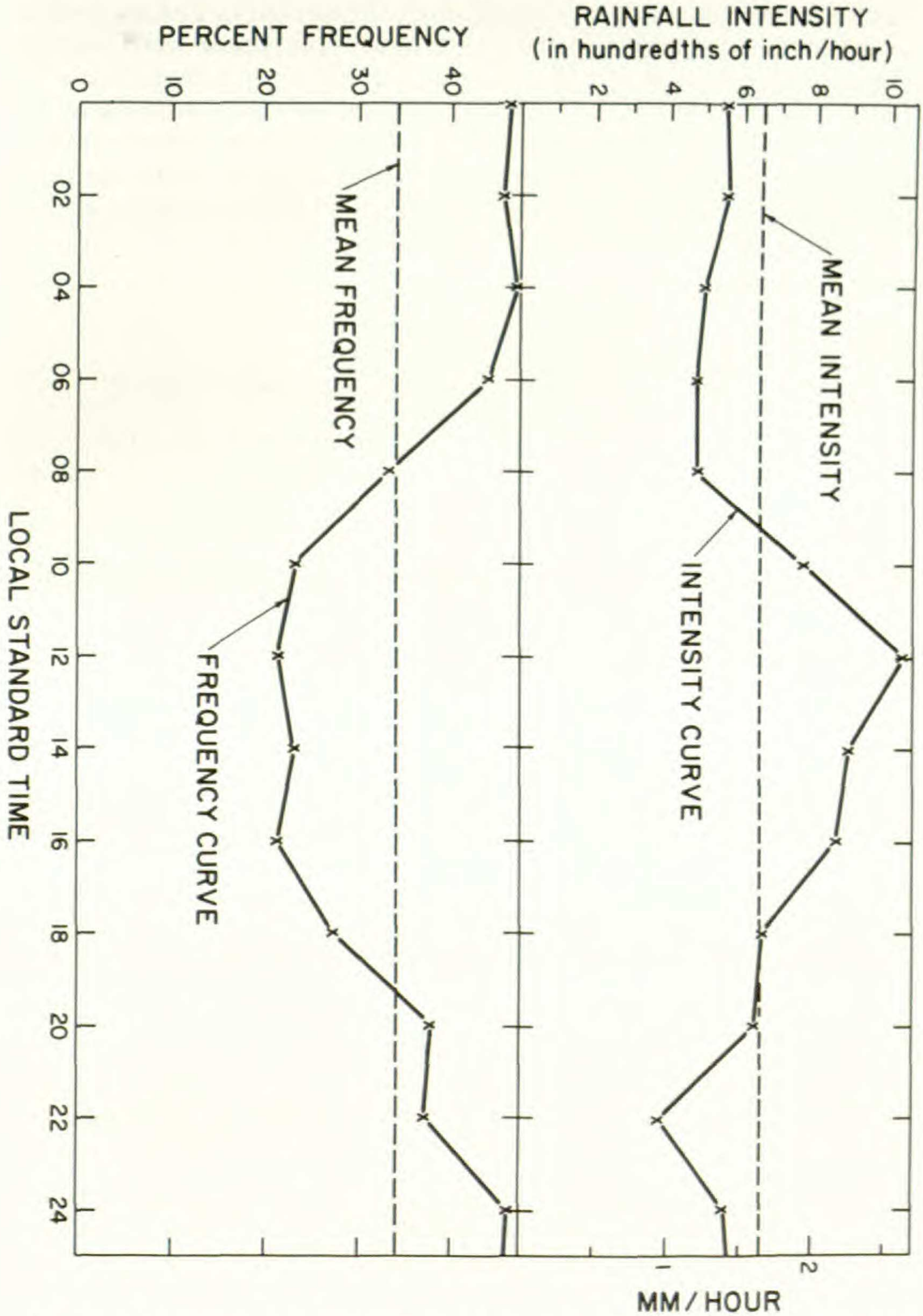

FIG. 3. A representation of the diurnal variation of intensity and frequency of rainfall occurrences.

night as in the day, whereas daytime rains were almost twice as heavy as nighttime rains. Presumably daytime rains are predominantly convective, while nighttime rains are orographic.

The effect of the forest on rainfall rate is illustrated in FIGURE 4 where the 1-minute accumulations of rainfall above and below the forest are compared for a typical shower. During an 11-minute interval 0.54 inches of rain fell above the forest. Within a minute the rain began below the forest, continued for 12 minutes and totalled 0.38 inches. The forest acts like a filter, delaying the onset of rain at ground level, lessening the peaks and smoothing the variations of intensity, and prolonging the rain slightly as it drips from the leaves.

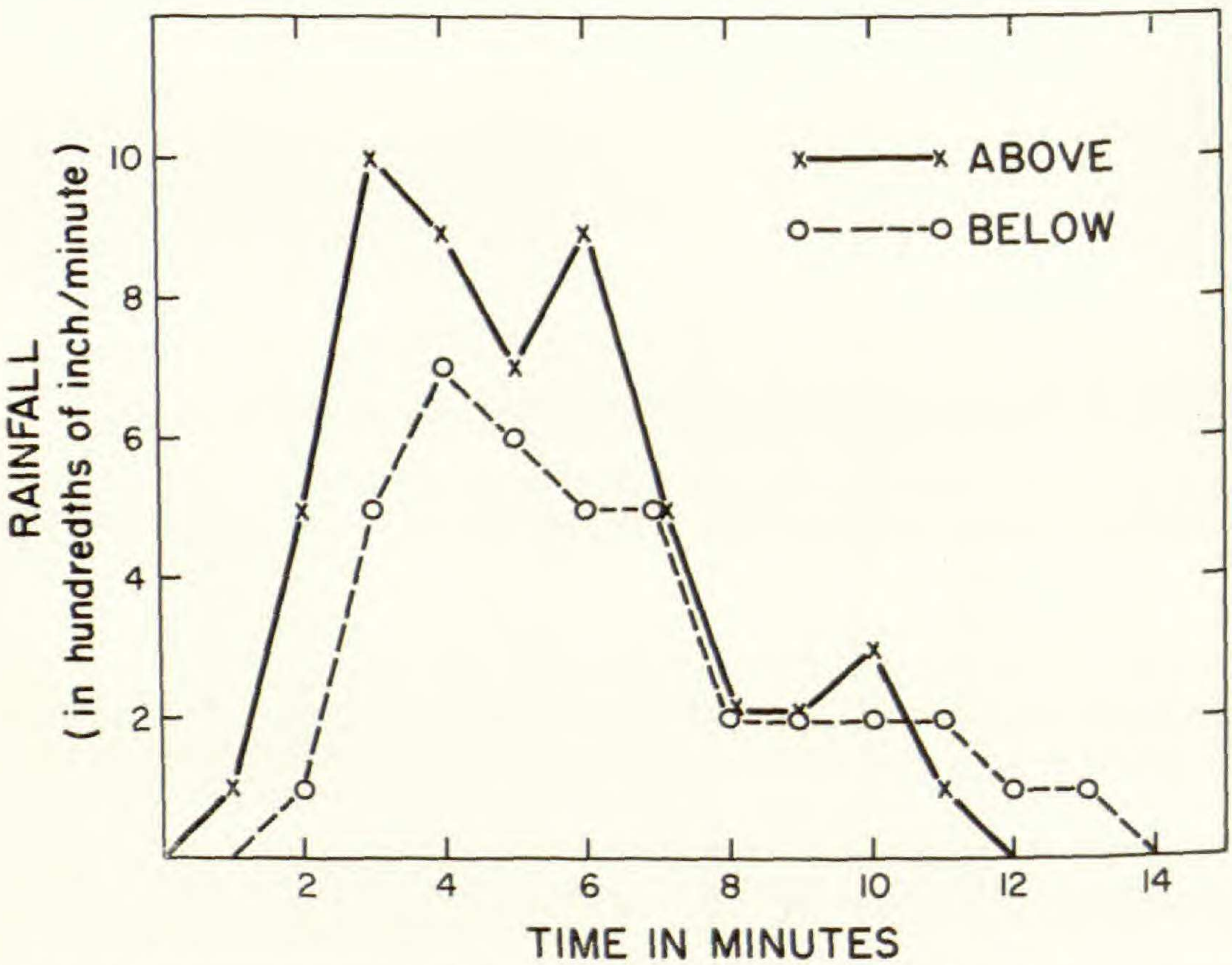

FIG. 4. A representation of the rainfall rate above and below the forest *versus* time, near noon, 20 July 1966.

The rain above that is not caught by the lower rain gage has either been intercepted by the trees or has reached the ground by means of the trunks. Hydrologists define interception as that portion of precipitation that never reaches the ground either as rain or trunk flow. This relationship is expressed in the simple continuity equation:

$$\text{Rain Below} = \text{Rain Above} - \text{Trunk Flow} - \text{Interception} \quad (1)$$

Wisler and Brater (1959) point out that after the initial wetting of the leaves, branches, and trunks of trees, the interception rate becomes equal to the evaporation rate from those surfaces. Since Pico del Oeste is usually shrouded in fog it follows that the interception rate is usually zero and that trunk flow must account for almost all of the difference between rain above and below the forest. This result contrasts with the rather large interception and small trunk flow reported by Clegg (1963) in much taller stands at lower elevations in the Luquillo Mountains.

Rainfall below the forest as a function of rainfall above was analyzed by standard regression techniques. One hundred and twenty-four rains were selected for the analysis. Each had the property that it was preceded by a 6-hour drying period as shown by the hygrograph trace. Thus part of each rain was used in wetting the foliage. The balance either ran down the trunks or dripped through. Using the notation X = rain above the forest in inches, Y = rain below the forest in inches, the analysis yielded:

$$Y = 0.768X - 0.034$$

with a correlation coefficient of 0.99 between X and Y.

A correction was dictated by slight differences in the volume of water required to tip the buckets in the two gages. The design value is 18.5 ml. Calibration of the two gages in place gave 18.5 for the upper gage and 18.9 for the lower gage. Appropriate adjustment leads to the final result:

$$Y = 0.786X - 0.035$$

On rewriting the equation in the form:

$$Y = X - 0.214X - 0.035$$

and comparing it to equation (1) we can identify trunk flow as 21.4 percent of the rain above and interception as 0.035 inches. Clegg cites other investigators as setting trunk flow no higher than 10 percent of the total rainfall. The explanation for large trunk flow on Pico del Oeste is undoubtedly found in the unusually high number of stems, a feature of this forest that is well illustrated in FIGURE 5.

The interception figure of 0.035 inches implies that the vegetation over each square meter of ground is able to store 886 ml/m^2. Studies of the U.S. Forest Service reported by Wisler and Brater indicate storage capacities of about 0.14 inch for hardwoods and 0.23 inch for pines in North Carolina. Storage in the cloud forest of Pico del Oeste would be expected to be very much less since it is only 10 to 12 feet high. It should be noted that, for rains occurring when the forest is already thoroughly wet, the relationship between rain below and above simplifies to

$$Y = 0.786X$$

Cloud Water. The difficulty with all cloud water studies is to relate the observations of a collecting device to the amount of water that the foliage itself extracts from the cloud. Although the same difficulty besets the interpretation of the data collected on Pico del Oeste, different lines of argument support the conclusion that cloud-water is of secondary importance in this region of abundant rain. In the first place, cloud water is not a means of sustaining the forest during drouth since cloud-free periods coincide with rainless periods. Secondly, four distinct analyses, each of which by itself is imprecise, give very similar results.

FIRST ANALYSIS. The cloud-water sampler was in service for 258 days during the year from June 1966 to May 1967. By extrapolating the data

FIG. 5. A view of the elfin forest illustrating the great number of stems in its composition.

to a full year the annual total of cloud water is estimated at 325 liters/square meters (l/m^2). Since 1 mm. of rain is the same as 1 l/m^2, the annual rainfall total of 453 cm. may be expressed as 4530 l/m^2. Although the unit cross section is in a vertical plane for cloud water and in a horizontal plane for rain, no adjustment is needed for trees such as those on Pico del Oeste that present about equal cross sections on horizontal and vertical planes. Moreover the wind speed through the thermometer shelter housing the cloud-water collector was found to be nearly the same as the wind in the forest halfway to the top, namely 17.6 and 16 percent, respectively, of the 20-foot wind. Deferring for the moment any discussion of differences in the collection efficiency of the aluminum shadescreen and the foliage, and differences in the sampling period, the data imply that cloud water is only 7.2 percent of rain water.

SECOND ANALYSIS. Another approach was based on a 1,000-hour period from 18 July to 29 August 1966. Since cloud water intercepted by the trees contributes to rain measured below the forest, the record of the 20-pen event-recorder was examined for occurrences of rain below the forest without rain above. The event of interest, "rain below without rain above," was defined as no rain above during the three hours including the hours preceding and following an occurrence of rain below. Any run of three hours without rain above the forest is a possible occurrence of the event of interest. There were 324 possible occurrences and only 15 observed occurrences. During the 1,000 hours the total rainfall below the forest was 15.83 inches. Of that total 0.15 inch occurred without rain above and must therefore be attributed to cloud water. Additional cloud water is also collected during rain but the exact amount cannot be determined. Again the implication is that cloud water is only a small fraction of rain water.

THIRD ANALYSIS. The 15 cases were then examined in detail in an attempt to relate the observed cloud water collection to the observed rainfall below the forest. The approach was to count the number of tips of the cloud-water collector during the time for 0.01 inch of rain to accumulate in the below-canopy rain gage. The data are summarized in TABLE 1. The entry for August 19 is suspect because of the long accumulation time indicating that the foliage must have dried out and had to be rewetted before the process of foliage drip could resume. The same might be true for August 16. The analysis is imprecise because in many cases some rain fell during the accumulation time. Omitting August 19 the mean is 5.4 units of cloud water per 0.01 inch of rain below the forest.

Earlier it was shown that 78.6 percent of rainfall drips through when the foliage is wet and the same will be true for cloud water. Thus the collection of $\frac{18.9}{18.5} \times 0.01$ inch[1] or 259 ml/m^2 of water below the canopy

[1] $\frac{(18.9)}{(18.5)}$ is the correction factor that accounts for 18.9 ml. being the actual volume of water to tip the bucket rather than the design volume of 18.5 ml.

during a rainless period results from the collection of $\frac{259}{0.786} = 330$ ml/m^2 of cloud water by the foliage. During the same period this analysis shows that 5.4 (50) = 270 ml/m^2 of water were collected by the cloud-water detector. Therefore, the foliage is 1.2 (i.e. 330/270) times as efficient as the cloud-water collector.

TABLE 1. **For fifteen occurrences of 0.01 inch rain below the forest without rain above, the amount of cloud water collected during the accumulation time, and the accumulation time.**

Date	Amount cloud water during accumulation time	Accumulation time for 0.01 inch rain below	
July 29	8.1 units *	4 hours	11 min
30	9.6	3	37
Aug. 2	6.6	4	50
2	5.4	4	30
5	5.0	3	12
5	1.2	1	40
7	1.4	3	12
9	7.3	3	43
11	2.5	3	9
13	4.2	5	14
13	4.0	4	54
14	5.5	4	17
16	10.0	11	8
19	16.5	24	39
22	5.0	3	10

* One unit, or bucket tip, equals 50 ml/m^2.

FOURTH ANALYSIS. The main shortcoming of the third analysis was the truncation error associated with the collection of rain and cloud water in discrete steps of a bucket. It appeared possible to sharpen the analysis by replacing the tipping buckets with bottles and measuring exact volumes of water collected by the two rain gages and the cloud-water collector under personally observed weather conditions. The fourth analysis summarizes the results of this approach carried out in December of 1967.

Five separate attempts were made to collect rain and cloud water under known boundary conditions. When the data were analysed, errors in experimental technique became evident. Generally there was doubt about the boundary conditions. No interpretation of the first attempt was possible because it became apparent that the foliage was neither fully wet nor fully dry. Another error in technique may be illustrated by the analysis of the data collected on 9 December.

The collecting of water began at 9:55 a.m., immediately after a moderate shower, and continued until 4 p.m. The error in technique was that the sampling began so soon after the shower that its effect was still being felt as drip from the foliage. The collected water was equivalent to 3227 ml/m^2 of rain above the canopy, 2746 ml/m^2 below the canopy, and only 70 ml/m^2 of cloud water. Because the foliage was always fully wet the relationship

$$Y = 0.786X$$

should apply where Y = 2746 ml/m^2. But because of the faulty technique, we have

X = Rain Above + (Cloud Water) E + $\triangle$R, with E being the ratio between the collecting efficiency of the vegetation and the cloud-water collector, and $\triangle$R being the unknown amount of rain above the canopy immediately before 9:55 that is in the process of getting to the ground via trunks and drip-through. Substituting both Y and X in the equation gives:

$$2746 = 0.786\ (3227 + 70E + \triangle R)$$

whence:

$$E = 3.82 - 0.014\ \triangle R$$

We conclude therefore that E is less than 3.82 since $\triangle$R is not zero, but that is all we can say.

Two of the attempts were for periods that began with dry foliage, i.e. no liquid water attached to plant surfaces. The collections in the three gages should therefore be related by:

$$Y = 0.786X - 886$$

where the units of X and Y are ml/m^2 so that 886 replaces 0.035 in the original equation because each hundredth of an inch of rain = 254 ml/m^2.

Between 4:35 p.m. December 7 and 1 p.m. December 8 the amounts collected were 3570 ml/m^2 of rain above, 2004 ml/m^2 below, and 16 ml/m^2 of cloud water. With so little cloud water the equation is too sensitive to slight errors in the collected amounts above and below to permit estimates of E, the relative collecting efficiency of the vegetation. We can, however, get independent estimates of the Y-intercept, 886, by substituting E = 1.2, the value obtained earlier or E $<$ 3.82,[2] the upper limit. These choices of E yield a Y-intercept = 817 and $<$850.

Conditions were also dry on the peak at 11:45 a.m. December 3 when collections were begun. By 3:45 p.m. December 4 the amounts were 1936 ml/m^2 of rain above, 906 ml/m^2 below, and only 22 ml/m^2 of cloud water. Setting E = 1.2 and $<$3.82 gave values of 637 and $<$682 for the Y-intercept. The average of these two trials was 727 for E = 1.2 and $<$766 for E $<$3.82, providing fair confirmation of the value, 886, obtained from the regression equation.

One attempt combined enough cloud water with light rain to permit an estimate of E, the relative collecting efficiency of the forest. Between

[2] $<$ is the symbol for "is less than."

4:30 p.m. on December 2 and 11:20 a.m. on December 3 the observed collections were 2128 ml/m^2 of rain above, 310 ml/m^2 of cloud water, and 1151 ml/m^2 of rain below. On December 2 the peak had been clear for four hours during the day but had fogged in shortly before 4:30 p.m.

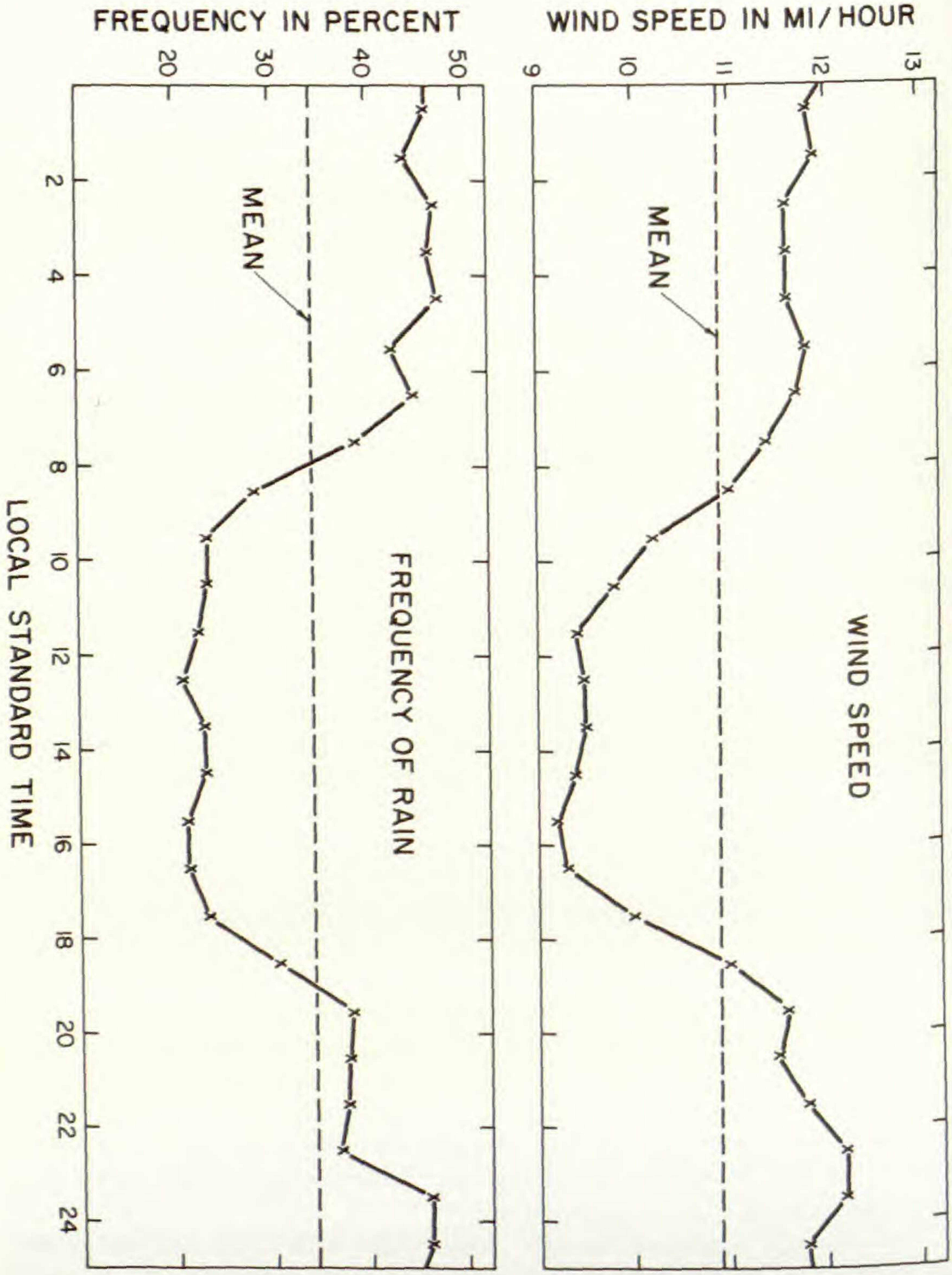

FIG. 6. A graphic comparison of the diurnal variations of wind speed and frequency of rain.

Presumably the forest was substantially, but not fully, dry. Substitution in the regression equation gives:

$$1151 = 0.786\ (2128 + 310\,\mathrm{E}) - 886,$$

from which E = 1.5 or slightly less since the constant, 886, is for fully dry foliage.

While not providing the hoped for "acid test," the fourth analysis confirms that the foliage is only slightly more efficient than the cloud-water collector and that its storage capacity is substantially less than that reported for other forests.

Correcting the first analysis for the greater collecting efficiency of the foliage, we have annual cloud water of 1.2 (325) = 390 l/m^2, which is 8.6 percent of the annual rainfall. Although this amount is relatively unimportant to the water budget of Pico del Oeste it is equal to the normal annual precipitation for Denver, Colorado.

Wind Speed. The diurnal variation of wind speed above the forest is shown in the upper half of FIGURE 6. The data were for a month with little daytime clearing, August, and a month with considerable daytime clearing, October. Both months showed the same pattern and were therefore combined. For comparison the diurnal variation of rainfall frequency is included in FIGURE 6. The night maximum and day minimum show the influence of convection. During the daytime there is a downward flux of mo-

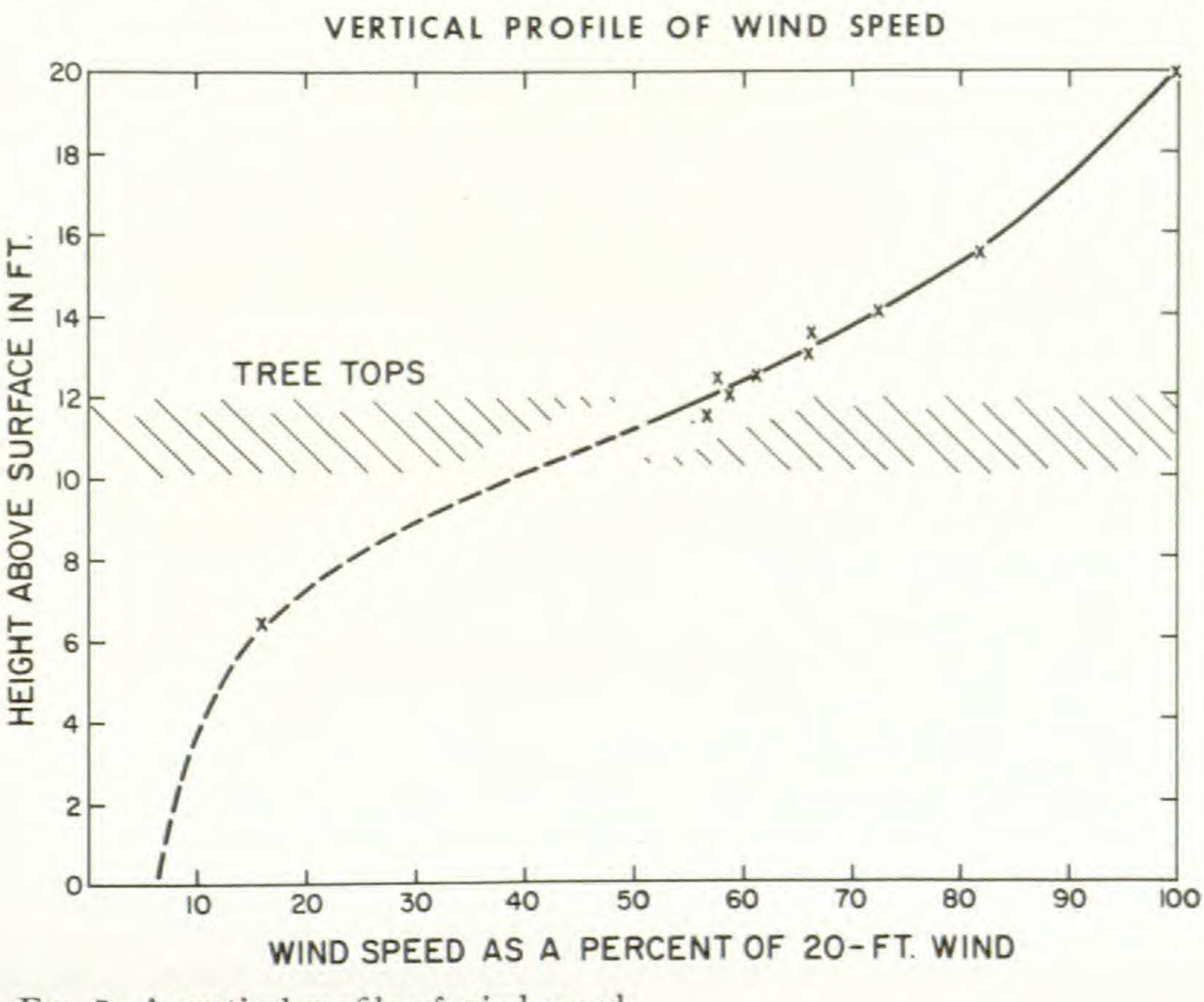

FIG. 7. A vertical profile of wind speed.

mentum below the mountain top and a consequent decrease in wind speed. The same anomalous cycle has been reported on towers several hundred feet above flat ground.

The almost identical cycle of rainfall frequency supports the interpretation that the frequent nighttime rains are mainly orographic, and that daytime rains are mainly convective.

The vertical profile of wind speed above and below the tree tops was investigated by installing a sensitive Casella anemometer at various heights on the tower. Wind speed averaged over an hour was expressed as a percent of the 20-foot wind. The results are presented in FIGURE 7. Additional points below the tree tops might modify that portion of the curve.

SUMMARY

Rainfall on Pico del Oeste, although twice as frequent by night, is only half as intense as during the day. Rain is mainly orographic by night and convective by day.

Trunk flow accounts for 21 percent of the rainfall.

The canopy has a storage capacity equal to a depth of 0.035 inches or 886 ml/m^2.

On the average, water extracted from the clouds by the foliage is slightly less than 10 per cent of rainfall.

Winds are strongest at night and weakest during the afternoon.

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 4. TRANSPIRATION RATES AND TEMPERATURES OF LEAVES IN COOL HUMID ENVIRONMENT[1]

DAVID M. GATES

THE PURPOSE OF THE STUDIES reported here is to contribute some understanding of the adaptation, growth, and behavior of plants in the mist forest at the top of Pico del Oeste, Luquillo Mountains, Puerto Rico.

The primary influence of climate on a plant is through the transfer of energy. All physiological processes consume energy. Biochemical reactions are temperature dependent and some are light dependent. The vitality of a plant depends on its temperature and its energy content. If a plant is too warm, its vital processes slow down; and above certain temperatures many physiological processes stop and denaturation of proteins occurs. If a plant is too cool, its vital processes slow down. The plant will not survive below certain temperatures. Most plants grow best at an optimum temperature.

The energy content of a plant determines its temperature. Several factors affect the energy exchanged between a plant and its surroundings. The significant environmental factors are radiation, air temperature, wind and humidity. In order for these factors to be translated into their effect on the plant, they must be expressed as energy flow. The incident radiation is a specific amount of energy. The air temperature and wind speed are translated into energy flow by the concept of convection. The humidity of the air affects the energy exchange for a leaf by means of the transpirational cooling. The leaf temperature and transpiration rate are dependent variables which are functions of the four independent variables: radiation, air temperature, wind, and humidity. Therefore, it is seen that one must deal with a six-dimensional problem. This is complicated, but there is no choice. It is not valid to ask for the influence of air temperature on transpiration rate without specifying the values of all other variables simultaneously. It is this simultaneity of factors which makes ecological problems complex.

ENERGY EXCHANGE

A leaf absorbs an amount of radiation which is designated Q_{abs} in cal cm^{-2} min^{-1}. The absorbed radiation is the sum of absorbed direct sun-

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light, scattered skylight, reflected light, and emitted thermal radiation from ground, vegetation, and atmosphere. The leaf absorbs each incident stream of radiation according to the absorptivity of its surface and the leaf orientation. This is discussed by Gates (1968a) in detail. The leaf consumes a very small fraction, maybe one or two percent, of the absorbed radiation in photosynthesis. The major portion of the absorbed radiation is lost by radiation emitted from the leaf surface, by convection and by transpiration. The energy budget for the leaf is given as follows:

$$Q_{abs} = \epsilon \sigma T_l^4 + k\left(\frac{V}{D}\right)^{1/2} (T_l - T_a) + L \frac{{}_sd_l(T_l) - r.h.\ {}_sd_a(T_a)}{r_l + r_a} \quad (1)$$

where ϵ is the emissivity of the leaf surface, σ is the Stefan-Boltzmann radiation constant, k is a constant, V is the wind speed in cm sec^{-1}, D the width of the leaf in cm, T_l and T_a the leaf and air temperatures respectively, L the latent heat of vaporization of water (580 cal gm^{-1} at 30°C), ${}_sd_l$ (T_l) and ${}_sd_a(T_a)$ the saturation vapor densities at the leaf and air temperatures respectively, r.h. the relative humidity of the air, and r_l and r_a the diffusion resistance of the stomatal pathway and adhering boundary layer of air on the leaf surface respectively. The value of r_a is inversely proportional to the wind speed and proportional to the leaf size. These factors are discussed more thoroughly by Gates (1968b). The energy budget is balanced by the leaf temperature adjusting to a value such that the energy into the leaf equals the energy out from the leaf. The leaf does this automatically for any conditions. We must use a computer to solve Eqn. (1) for the temperature and transpiration rate for any set of conditions.

CLIMATE OF PICO DEL OESTE

The purpose here is to make a reasonable estimate of the transpiration rate of the plants at the summit of Pico del Oeste, Luquillo Mountains, Puerto Rico. In order to estimate transpiration rate one needs to know the climate to get values of radiation, air temperature, wind speed, and humidity. The climate of El Yunque Mountain in the Luquillo Mountains is reported by Briscoe (1966) and for Pico del Oeste meteorological observations are reported by Baynton (1968) and by Howard (1968). The climate of the peak is generally wet with frequent rain and mist, windy, temperate, and of low illumination. TABLE 1 summarizes the climate and is an approximate indication of the conditions expected. The mean wind speed at tree top level on the peak is 14 mph. The incident global radiation on a horizontal surface has a maximum value of 0.8 cal cm^{-2} min^{-1} on the peak as compared with 1.3 cal cm^{-2} min^{-1} at San Juan. There is no question that the peak has a low light level as the result of the persistent cloud cover. Briscoe's measurements for El Yunque show it to have a mean wind speed of 13 mph and a mean relative humidity of 98 percent. The maximum radiation at noon on El Yunque was 0.8 cal cm^{-2} min^{-1}, with a minimum of about 0.3 cal cm^{-2} min^{-1}.